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Rapid Gain Adaptation Affects the Dynamics of Saccadic Eye Movements in Humans

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The effect of rapid gain adaptation on the dynamics of visually guided saccades was investigated in six human subjects by using a search coil system. Saccadic adaptation was induced artificially by dislocating the target (by about 30% of the initial step) either forward (gain increase) or backward (gain decrease) during the primary saccade ("double-step paradigm"). Duration, peak velocity and peak acceleration and deceleration of a "standard 12 deg saccade" were computed from the data and were compared for the conditions of gain decrease, gain increase and the control without gain adaptation. The gain as well as the peak velocity and duration of the saccades showed an increased variability during the adaptation. In general, the abducting saccades had a higher peak acceleration than the adducting saccades, and all subjects showed an idiosyncratic pattern of the acceleration and deceleration. In the gain increase paradigm the subjects showed an increase in the duration and a decrease in the peak velocity. In the gain decrease paradigm there was a significant smaller ratio of peak acceleration/peak deceleration compared to the gain increase and the control condition. The findings demonstrate that rapid gain adaptation influences the dynamics of saccades in a specific way: peak saccadic velocity decreases and duration increases in the gain increase paradigm and peak acceleration/peak deceleration decreases in the gain decrease paradigm. Moreover, these results also suggest that the deceleration is neuronally controlled and not merely a result of mechanical constraints.

Saccade adaptation Double-step paradigm Saccade duration Saccade peak velocity Saccade peak acceleration

INTRODUCTION

Saccades, which are considered to operate in an open-loop way, are highly accurate throughout life. However, since there is lifelong neuronal loss in the oculomotor system and changes in the mechanics of the eyeball (Becker, 1989), they must continually adapt. This adaptation process can be investigated in the laboratory by requiring a subject to make saccades to a target that moves systematically forward or backward during the saccade (McLaughlin, 1967; Deubel, Wolf & Hauske, 1986; Deubel, 1987). Such a paradigm allows the investigator to increase or decrease saccadic gain (defined as the ratio of saccade magnitude and target eccentricity) after 100–500 trials in humans. Whether such gain adaptation also changes the dynamics of the saccades is still an open question. Some investigations found a change in the peak velocity/amplitude ratio (Abrams, Meyer & Kornblum, 1989; Fitzgibbon, Goldberg & Segraves, 1986); others did not (Albano & King, 1989). One reason for this disagreement is that the amplitudes of the saccades change during the adaptation; consequently, their peak velocity and duration also change. Furthermore, since several hundred saccades must be performed during adaptation, fatigue may also influence the dynamics of the saccades. All these factors make an experimental approach difficult.

Nevertheless, an answer to this question may provide insight into the mechanisms and brain structures involved in rapid gain adaptation of saccades. If there is a change in the dynamics of saccades, then adaptation may change the function of the saccade burst generator, not just the parametric inputs to the burst generator. Recent findings suggest that the caudal fastigial nucleus (cFN) influences the acceleration and deceleration of visually guided saccades (Fuchs, Robinson & Straube, 1993; Robinson, Straube & Fuchs, 1993). A change in the acceleration/deceleration of the saccades during gain adaptation would imply the involvement of the cFN in the adaptation of saccades.

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We investigated the effect of rapid gain adaptation on the dynamics of saccades. In order to eliminate the problems of amplitude changes and fatigue, we applied a new paradigm in which saccadic parameters were determined for a "standard 12 deg saccade", after gain increase, gain decrease and under control conditions.

MATERIALS AND METHODS

Subjects

Six adult human subjects (mean age 32.0 ± 7.1 yr) participated in the experiments. After giving their informed consent, each subject was tested at least three times (gain increase, gain decrease and control condition) on different days. All subjects were experienced in oculomotor testing, but only two of them (the authors) were aware of the goal of the investigation. The visual acuity of the subjects was at least 20/20 with correction.

Stimulus presentation

A red laser served as visual stimulus. It was driven by means of two fast servo-controlled x–y galvanometer scanner motors (Laser Scanning Keiser AG, Stallikon), which were driven by an analogue signal synthesized by a D/A-converter under the control of a PC (Intel 486 processor). The PC also provided automatic off-line analysis of the eye movement data. The laser spot was projected on the back of a translucent planar screen 1.5 m in front of the subjects. The target jumped with random amplitudes of 6, 9, 12 and 16 deg, either to the right or left, the final position then becoming the starting position for the next trial. The target never appeared with more than 20 deg eccentricity. After 100 saccades, which served as a preadaptation control (data not shown), the subjects performed 400–500 adapting saccades. In the control sessions, no intrasaccadic target displacement was elicited. In the adaptation sessions, the target was artificially shifted backward [Fig. 1(a)] or forward during the primary saccade by 30% of the initial step size. In the gain increase sessions the size of the initial target step was selected randomly from 6, 9 and 12 deg; in the gain decrease experiments the sizes were 9, 12 or 16 deg. This ensured that the saccadic amplitude distribution in the control session [no displacement, Fig. 1(b)] was comparable with that in the adaptation session. The eye movements were digitized on-line, and the computer detected the ongoing saccade by using a velocity criterium. The intrasaccadic target displacement occurred when instantaneous eye velocity exceeded 30 deg/sec.

Eye movement recording and analysis

Eye movements were measured by an electromagnetic scleral coil technique. The subject was placed in the centre of a 70 × 70 × 70 cm horizontal and vertical magnetic field (Skalar, Delft). The subject's head was stabilized with a forehead and chin rest. A standard two-dimensional silicon contact coil (Skalar, Delft) was placed on the sclera after anaesthesia of the right eye. The subject's eye movements were calibrated at the beginning of each session by sequential fixation of 10 positions arranged 12 deg apart on a circular array around the central fixation spot. After calibration, the overall accuracy of the system was better than 5 min arc and the signal/noise ratio better than 1 min arc (see also Fig. 1).

The signals representing horizontal and vertical eye position were sampled with a resolution of 12 bits at 500 Hz and were stored on a hard disk together with the target position for later off-line analysis. The gain, peak velocity [Fig. 1(c)], peak acceleration and peak deceleration [Fig. 1(d)] for each individual saccade were calculated on the basis of filtering the eye position signals by a combination of ideal digital differentiators and a second-order bandpass filter. The bandwidths of the digital differentiators were 125 and 100 Hz for velocity and acceleration respectively. For the computation of saccade duration, times of onset and offset of the saccade were determined as the points of intersection of regression lines calculated within temporal windows of 20 msec during, immediately before and after the saccade.

To produce a standard saccade for comparison, the peak velocity/amplitude ratio, the peak acceleration or deceleration/amplitude ratio and the duration/amplitude ratio were normalized by fitting the saccades of each adaptation session for each subject by an exponential fit $[v(A) = v_0 - v_1 \times (1 - \exp(-A/v_t)]$ (amplitude to peak velocity and amplitude to peak acceleration) [Fig. 1(f–h)] or in the case of amplitude to duration with a linear fit $(D = D_0 + D_1 \times A)$ [Fig. 1(e)]. For this analysis the first 150 saccades of each adaptation or control session were discarded. By doing so we could characterize the dynamics of the saccades (overview in Becker, 1989) during adaptation and then determine the dynamics of a standard 12 deg saccade during adaptation for each subject [Fig. 1(e–h), dashed lines]. This standard 12 deg saccade was then used to compare the behaviour of the six subjects during the different test conditions. Figure 1 shows the fits and the "raw data"; the data fit quite well. This ensures that the standard 12 deg saccade can also be used to describe the behaviour of the data.

In order to evaluate the quality of data fit, we also calculated the SDs of the residuals after the fitting [e.g. error bars in Fig. 1(h)]. It should be emphasized that due to the large number of data points in each fit, the 99% confidence intervals for the estimated parameters of our standard 12 deg saccade were very small; typical values were in the range of 0.6 msec, 3 deg/sec and 200 deg/sec^2 for duration, velocity and acceleration respectively. Moreover, since data analysis showed that the residuals are independent of saccade amplitude, similar results can be expected for other "standard saccade" sizes.

RESULTS

General behaviour

All subjects tested showed a considerable amount of adaptation during the gain decrease paradigm (Fig. 2, ○), while saccadic gain was constant in the control condition

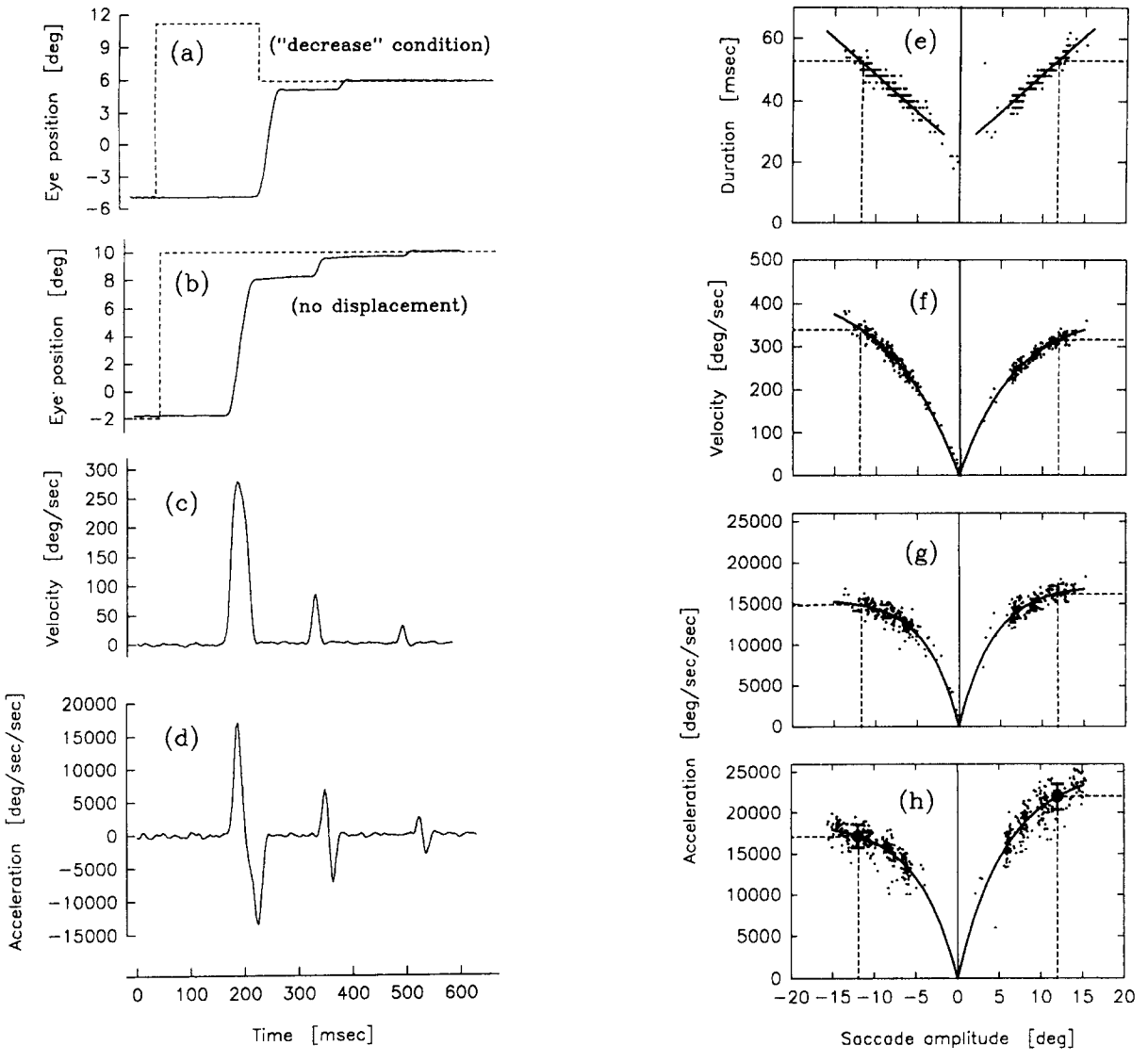

FIGURE 1. (a, b) Examples for stimulus and eye position traces in the "gain decrease" and "control" conditions. The dashed lines indicate the position of the target, the solid lines indicate the horizontal eye position. Note that the initial target position can vary depending on the final target position after the preceding trial. (c, d) First and second derivatives of the eye position signal (velocity and acceleration). Note the low noise levels even in the acceleration signal. (e–h) Typical saccade duration, peak velocity and peak acceleration data given as a function of saccade amplitude and direction [(e–g) subject MF; (h) subject JB]. The solid lines represent the results of linear and exponential fitting of the data points. The dashed lines indicate the characteristic parameters for a standard 12 deg saccade derived from the analysis.

(Fig. 2, □). Thus, after 300–400 adapting saccades the gain was decreased by 20–25%. In contrast, during the gain increase paradigm most of the subjects (five of six) adapted only slightly (5–10%); only one subject (HD) was able to increase his gain by more than 10% (Fig. 2, ●). Furthermore, there was a considerable amount of variability of the gain during the adaptation which is indicated by the SD of the running average.

Saccade acceleration/deceleration

Figure 3 shows the peak acceleration (○) and peak deceleration (●) as a function of saccadic amplitude during the control condition for the six subjects. Abducting saccades are plotted as positive amplitude values; adducting saccades as negative values. We were surprised to find that each subject had his own idiosyncratic "fingerprint", which allowed us to identify the subject on the basis of typical asymmetries of the ratio for peak acceleration to amplitude and peak deceleration to amplitude of abducting and adducting saccades. Overall, the abducting saccades had a higher peak acceleration than the adducting saccades. Five of the six subjects showed higher acceleration than deceleration values. Surprisingly, one of the subjects (MF) produced higher values for the peak deceleration under all tested conditions.

Saccade duration

Figure 4 depicts the duration of the standard 12 deg saccade for the gain decrease paradigm, the control condition without adaptation and the gain increase paradigm. The most consistent finding was the increase in duration of the adducting saccades during the gain increase paradigm in all six subjects and of the abducting

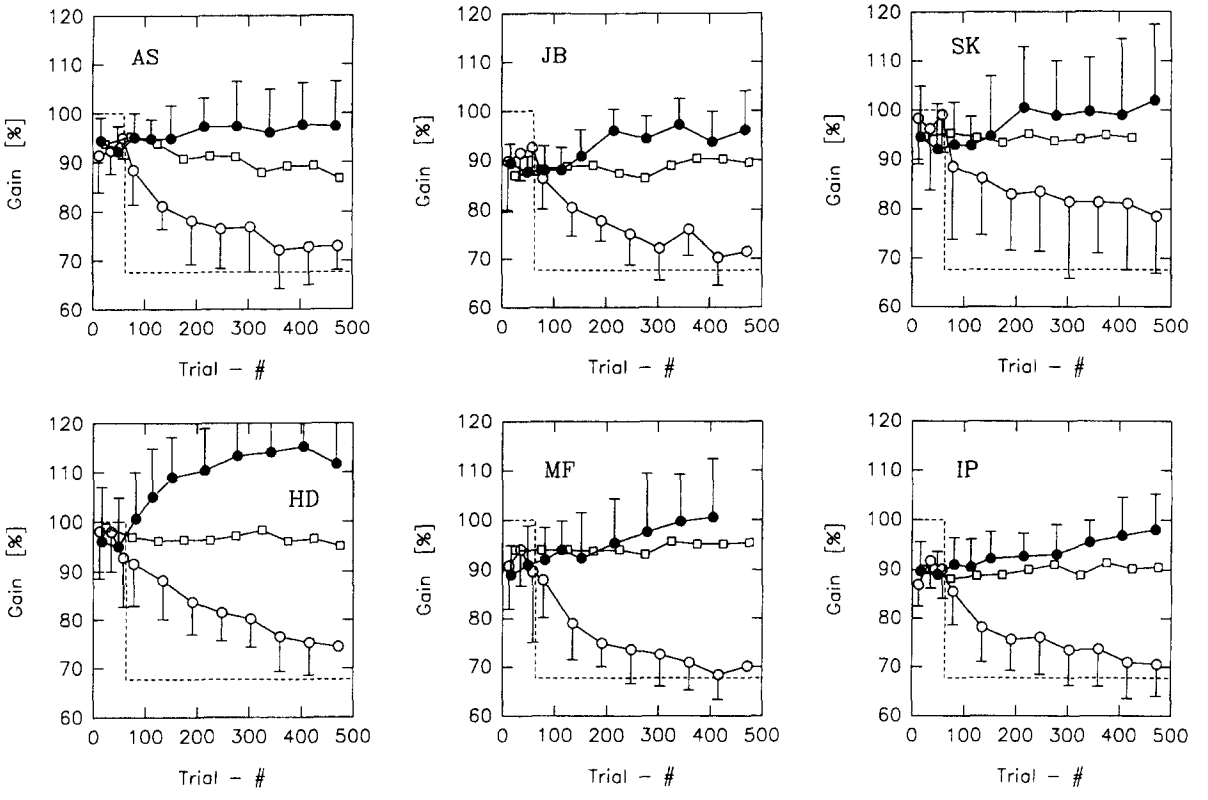

FIGURE 2. Running averages (every 50 saccades) and SD of saccadic gain during the gain increase paradigm (●), control condition (□) and gain decrease paradigm (○), shown for all six subjects.

saccades in five of the subjects, as compared to the control condition. An analysis of variance (ANOVA, repeated measures) revealed a significant main effect of the adaptation condition [$F(2,10) = 7.96$, $P < 0.01$]. *Post-hoc* Newman–Keuls tests showed that the Increase condition leads to significantly longer durations than the Control condition ($P < 0.05$). Decrease and Control conditions did not significantly differ however ($P > 0.05$).

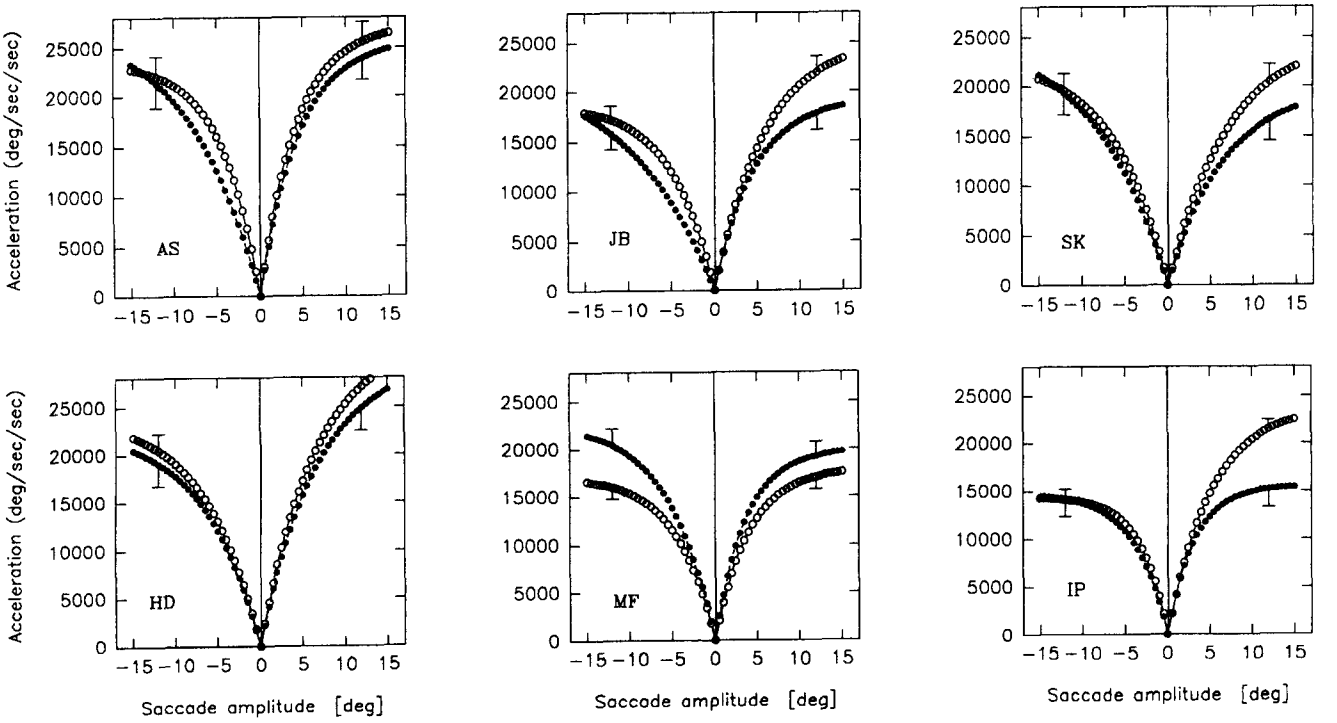

FIGURE 3. Results of the exponential fits of the experimental data for the acceleration (○) and deceleration (●) during the control condition. Abducting saccades are given positive amplitude values; adducting saccades in negative values. In five of the six subjects the acceleration of the abducting as well as the adducting saccade is higher than the corresponding deceleration.

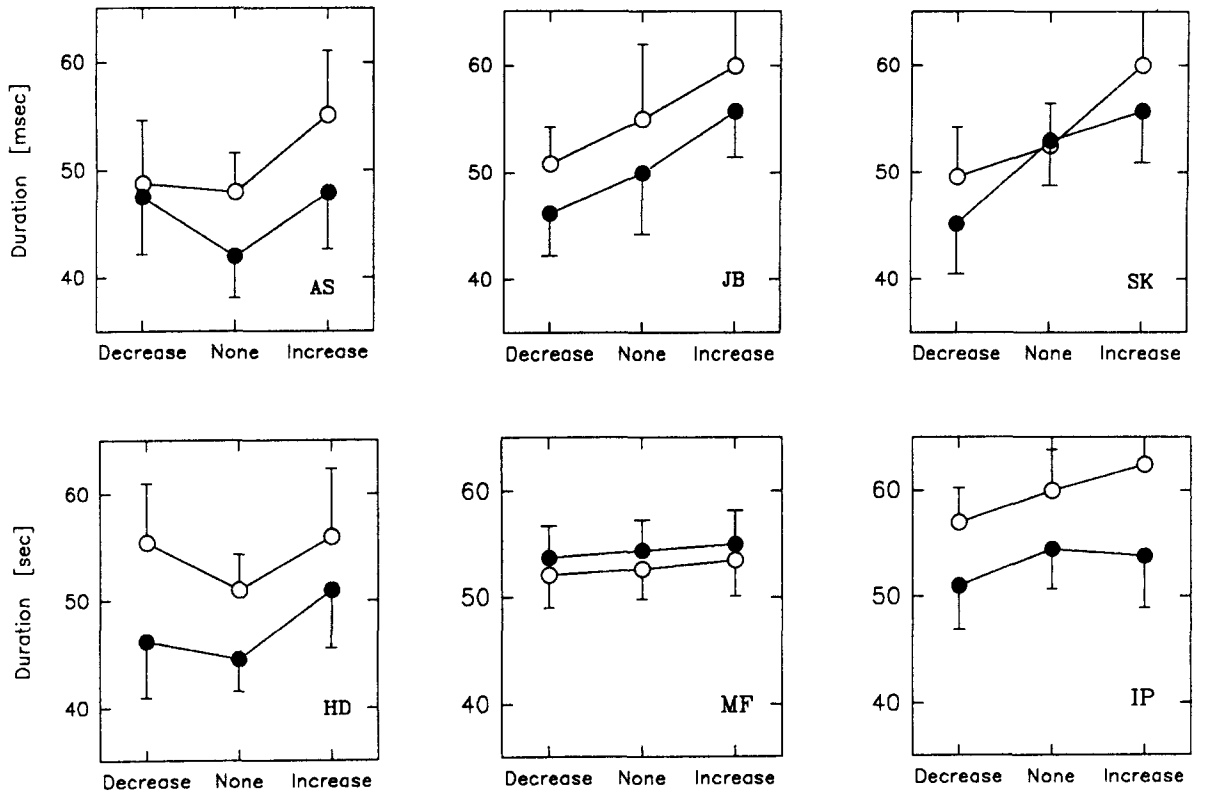

FIGURE 4. Mean duration of a standard 12 deg saccade in the gain decrease paradigm under the control condition and in the gain increase paradigm, presented for all six subjects (○ adducting saccades; ● abducting saccades). Error bars indicate the SDs of the residuals after the fit. In all subjects the duration increased during the gain increase paradigm.

Furthermore, five of the six subjects had a shorter duration for the abducting saccade than for the adducting saccade.

Saccade peak velocity

Another description often used for the dynamics of saccades is the peak velocity/amplitude ratio, which is presented analogically in Fig. 5. Corresponding to their longer saccade durations, all subjects tended to have lower peak velocities for a 12 deg saccade during the gain increase paradigm than during the control condition or the gain decrease paradigm. Indeed, ANOVA again revealed a significant main effect of the adaptation condition [$F(2,10) = 28.22$]. Newman–Keuls tests confirmed that velocities in the Increase condition are significantly smaller than in the Control condition ($P < 0.01$). Control and Decrease conditions do not differ significantly.

Peak acceleration/deceleration ratio

To investigate whether the skewness of the saccade changes depends on the paradigm, we also calculated the ratios of peak acceleration and peak deceleration. In general, the peak acceleration (during abducting as well as adducting) was slightly higher in five of the subjects than was peak deceleration. This results in ratios > 1. ANOVA demonstrated a significant effect of the adaptation condition [$F(2,10) = 5.89$; $P < 0.02$]. The ratio was significantly smaller for the gain decrease condition than for the control condition (Newman–Keuls test, $P < 0.05$). Acceleration/deceleration ratios did not differ between control and gain increase paradigm (Newman–Keuls, $P > 0.05$). Interestingly, only subject HD, who also showed the largest amount of adaptation (Fig. 2), had a larger ratio in the gain increase condtion than in the control condition.

DISCUSSION

During adaptation each subject tested showed a different change in saccadic duration and peak velocity, especially during the gain increase paradigm. It is not surprising that the amount of this change was quite variable, as this has also been observed in other motor learning paradigms (Jaric, Corcos, Agarwal & Gottlieb, 1993). In the gain increase paradigm the peak velocity decreased and the duration increased significantly for the standard 12 deg saccade. The change in the dynamics of the saccades was less in the gain decrease paradigm; however, all six subjects showed an increase in the peak velocity and a decrease of the duration compared to the gain increase paradigm. In contrast to the gain increase paradigm, there was no significant difference between the gain decrease paradigm and the control condition. Otherwise there was a significant influence of the gain decrease adaptation on the ratio of peak acceleration/peak deceleration with smaller values during the gain decrease condition. Furthermore, each subject showed an idiosyncratic acceleration and deceleration profile with higher values for saccadic acceleration than saccadic

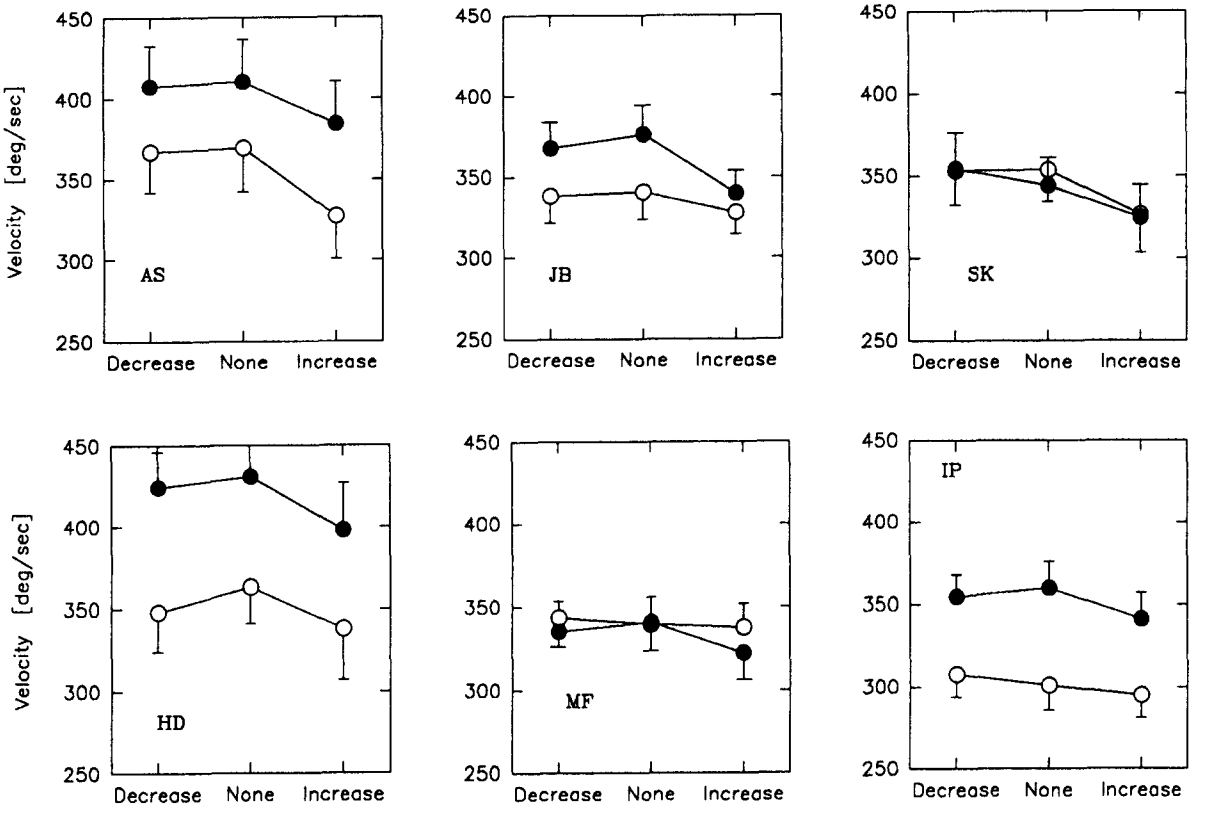

FIGURE 5. Peak velocity of a standard 12 deg saccade in the three adaptation conditions, given for the six subjects (○ adducting saccades; ● abducting saccades). Error bars indicate the SDs of the residuals after the fit. Peak velocities decrease in the gain increase paradigm in all subjects.

deceleration in five of six subjects. The different individual profiles support the idea that deceleration is also controlled neuronally as is acceleration.

To our knowledge, there are only four reports available in the literature which studied the dynamics of saccades during adaptation. None investigated the dynamics of saccades quantitatively during the gain increase and decrease conditions, nor did they compare these values with the same number of saccades under a control condition. In a short communication about saccade adaptation in monkeys, Fitzgibbon *et al.* (1986) reported several velocity maxima during forward adaptation. During gain decrease adaptation some saccades had higher than normal peak velocities at the beginning (see Fig. 2 of their publication), but later lower than normal velocities. However, this study did not present quantitative data. In our recordings we found saccades with multiple velocity peaks in only a few cases ($<1\%$).

In another study, Abrams *et al.* (1992) investigated the velocity time curves before and during gain decrease adaptation in humans. They found that the magnitude of the force pulse, corresponding to the peak velocity, was reduced and that the duration showed only small changes; however, due to the smaller amplitude of the adapted saccades the duration was unusually long. They concluded that the gain change is not due to remapping of target locations. Our results were similar to those of Abrams *et al.* (1992). Our six subjects also had smaller ratios for peak acceleration to peak deceleration than under the control condition (Fig. 6), corresponding to lower peak accelerations or higher peak decelerations during the gain decrease condition. However, unlike Abrams *et al.* (1992), we found that the saccades of four of the six subjects tended to have shorter than normal saccadic durations during the gain decrease condition. During the gain increase especially, paradigm saccades tended to have smaller than normal peak velocities and longer durations in our study. This suggests that in the gain increase condition it is not the force pulse that is

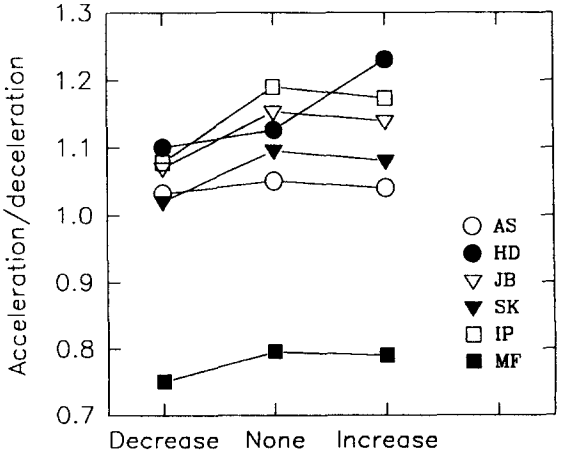

FIGURE 6. Peak acceleration/peak deceleration ratios in the three adaptation conditions, given for the six subjects. All subjects show smaller ratios for the Decrease than for the Control condition. Only subject HD reveals a higher ratio than the control in the gain increase paradigm.

primarily adapted, but rather the duration of the force pulse. In the gain decrease condition either the duration or the force pulse (acceleration) might be changed.

Contrary to the above studies and our results, Albano and King (1989) stated that the duration of the adapted saccades was consistent with the duration–amplitude characteristics of normal preadaptive saccades in humans. It is interesting to note that their gain decreased by only 10% in contrast to ours which, on average, decreased by 20–25%. Thus, adaptation could be expected to have only a weak effect on the dynamics of saccades, and consequently they did not detect any. No quantitative measurements or statistics were presented. Frens and van Opstal (1994) investigated the effect of a gain decrease adaptation of about 20% of the initial saccade amplitude on the skewness of the saccade (here defined as time to peak velocity/total saccade duration). They did not obtain evidence that the main sequence characteristics of the primary saccades changed during adaptation. However, they also described a slight tendency of the saccades to be less skewed (i.e. acceleration phase/deceleration phase tended to 1) during the adaptation. In the example given in their publication [Fig. 4(a, c)] there is a surprising increase in the peak velocity of the saccades performed directly after the end of adaptation (start of the readaptation). Another possible reason for their failure to detect an influence of adaptation on the saccade dynamics could be the use of only a gain decrease paradigm and the fact that with 10% or 20% their backstep was smaller than in our study (30%). Also, in our study the effect of the gain decrease paradigm on the dynamics of saccades was less than the effect obtained by the gain increase paradigm. It was only obvious when the ratio of peak acceleration to peak deceleration was analysed. Furthermore, these studies did not measure acceleration and deceleration as we did.

What is the reason for the difference in the influence of the dynamics between the gain increase and gain decrease adaptation?

We can only speculate on the reasons for the surprising finding that the dynamics are more influenced by the gain increase adaptation, although the measured gain change after 400–500 adapting saccades is less during the gain increase adaptation. One possible explanation is that we used only the last 450 saccades during the adaptation to calculate the fit. It is well known that the gain increase adaptation has a significantly slower time constant than the gain decrease adaptation (Deubel, 1991). Thus the last 450 saccades during the gain increase condition might have in average a larger remaining error than the last 450 saccades during the gain decrease condition (because of the shorter time constant of the adaptation). This on the average smaller remaining error in the gain decrease condition may be the reason why we observed less change in the saccadic dynamics in the gain decrease than in the gain increase condition. Another possibility is that during the gain increase condition the oculomotor system uses another strategy, i.e. to change the duration, than during the gain decrease condition, namely, to change the skewness.

Implications for the mechanisms involved in saccade adaptation

Our main finding is that not only a parametric gain adaptation, in other words, an adaptation of the command to the brainstem saccade generator, takes place during rapid gain adaptation of saccades. The finding that there is also an adaptation-specific change in the dynamics of the saccades suggests that the function of the brainstem generator itself changes during adaptation. Several groups recently reported that the neuronal discharge in the cFN during saccades correlates with the end of ipsilateral saccades. Thus, the neuronal discharge precedes the eye movement onset for small saccades but lags behind for saccades larger than 15–20 deg (Ohtsuka & Noda, 1991; Fuchs *et al.*, 1993; Helmchen, Straube & Büttner, 1994). On the basis of these reports and the finding that after deactivation of the cFN by local injection of muscimol the ipsiversive saccades were too large, Robinson *et al.* (1993) proposed that the cFN controls the acceleration of contralateral saccades and the deceleration of ipsilateral saccades. Such a mechanism is also suggested by the model of brainstem–cerebellar interaction of Dean, Mayhew and Langdon (1994). Using Kawato's principle of feedback-error-learning (Kawato, 1990), they located this feedback-controller in the posterior vermis/cFN. Their model predicts a similar change in the dynamics of the saccades as was seen after muscimol deactivation of the cFN (Robinson *et al.*, 1993). Thus, it is possible that the change seen in the acceleration and/or deceleration of saccades during adaptation reflects the influence of the cFN on the saccadic burst generator. This, together with the finding of Optican and Robinson (1980) that destruction of the vermis and possibly also the underlying cFN prevents saccade adaptation in monkeys, suggests to us that the posterior vermis and the cFN are fundamentally involved in the rapid gain adaptation of saccades.

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